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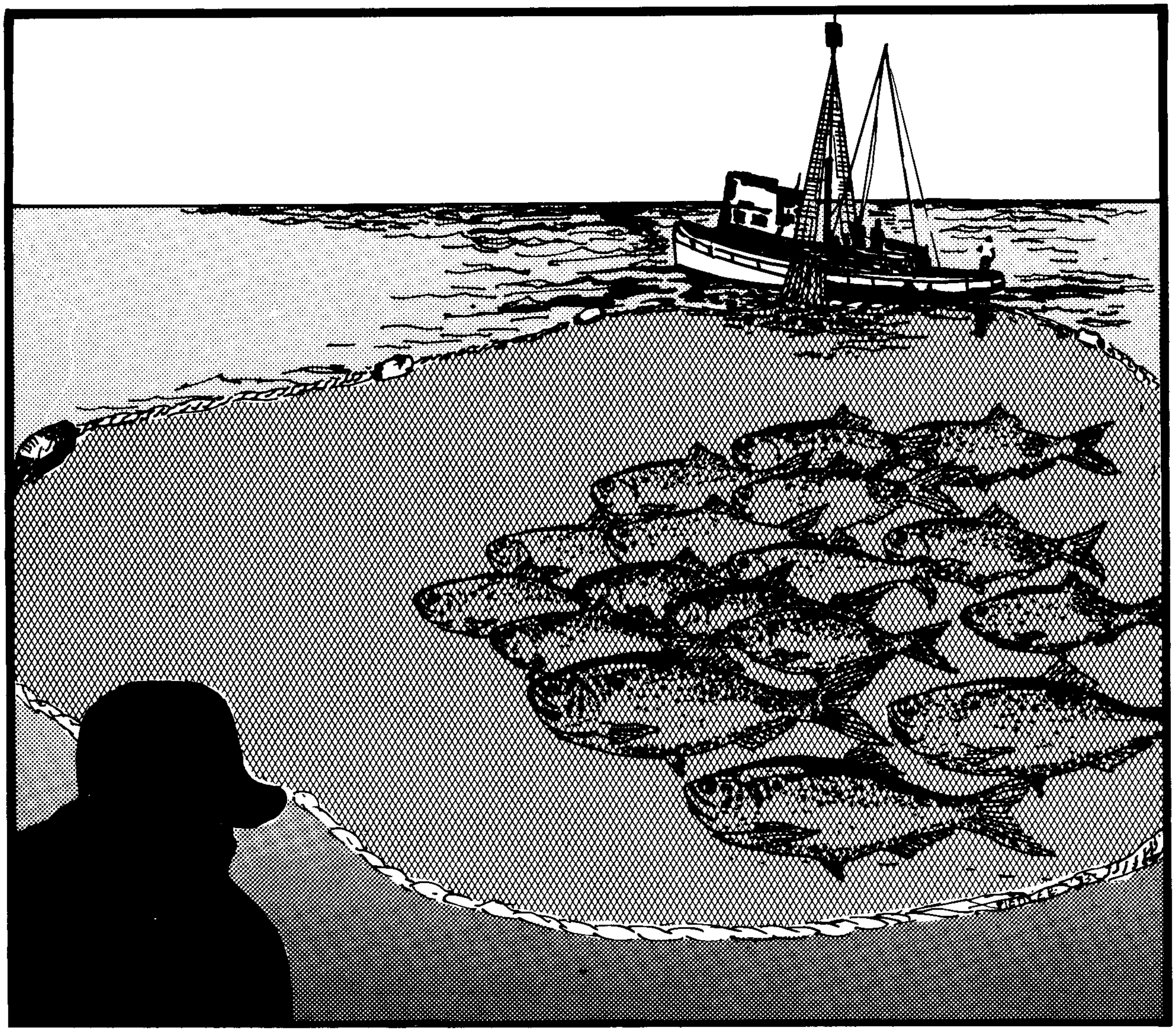

Fish and Wildlife Service
U.S. Department of the Interior

Coastal Ecology Group
Waterways Experiment Station
U.S. Army Corps of Engineers

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ATLANTIC MENHADEN

by

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CONVERSION FACTORS

Metric to U.S. Customary

Multiply	BY	To Obtain
millimeters (mm)	0.03937	inches
centimeters (cm)	0.3937	inches
meters (m)	3.281	feet
kilometers (km)	0.6214	miles
square meters (m^2)	10.76	square feet
square kilometers (km^2)	0.3861	square miles
hectares (ha)	2.471	acres
liters (1)	0.2642	gallons
cubic meters (m^3)	35.31	cubic feet
cubic meters	0.0008110	acre-feet
milligrams (mg)	0.00003527	ounces
grams (gm)	0.03527	ounces
kilograms (kg)	2.205	pounds
metric tons (mt)	2205.0	pounds
metric tons (mt)	1.102	short tons
kilocalories (kcal)	3.968	BTU
Celsius degrees	1.8(C°) + 32	Fahrenheit degrees

U.S. Customary to Metric

inches	25.40	millimeters
inches	2.54	centimeters
feet (ft)	0.3048	meters
fathoms	1.829	meters
miles (mi)	1.609	kilometers
nautical miles (nmi)	1.852	kilometers
square feet (ft^2)	0.0929	square meters
acres	0.4047	hectares
square miles (mi')	2.590	square kilometers
gallons (gal)	3.785	liters
cubic feet (ft^3)	0.02831	cubic meters
acre-feet	1233.0	cubic meters
ounces (oz)	28.35	grams
pounds (lb)	0.4536	kilograms
short tons (ton)	0.9072	metric tons
BTU	0.2520	kilocalories
Fahrenheit degrees	0.5556(F° - 32)	Celsius deqrees

CONTENTS

PREFACE

This species profile is one of a series on coastal aquatic organisms, principally fish, of sport, commercial, or ecological importance. The profiles are designed to provide coastal managers, engineers, and biologists with a brief comprehensive sketch of the biological characteristics and environmental requirements of the species and to describe how populations of the species may be expected to react to environmental changes caused by coastal development. Each profile has sections on taxonomy, life history, ecological role, environmental requirements, and economic importance, if applicable. A three-ring binder is used for this series so that new profiles can he added as they are prepared. This project is jointly planned and financed by the U.S. Army Corps of Engineers and the U.S. Fish and Wildlife Service.

Suggestions or questions regarding this report should be directed to:

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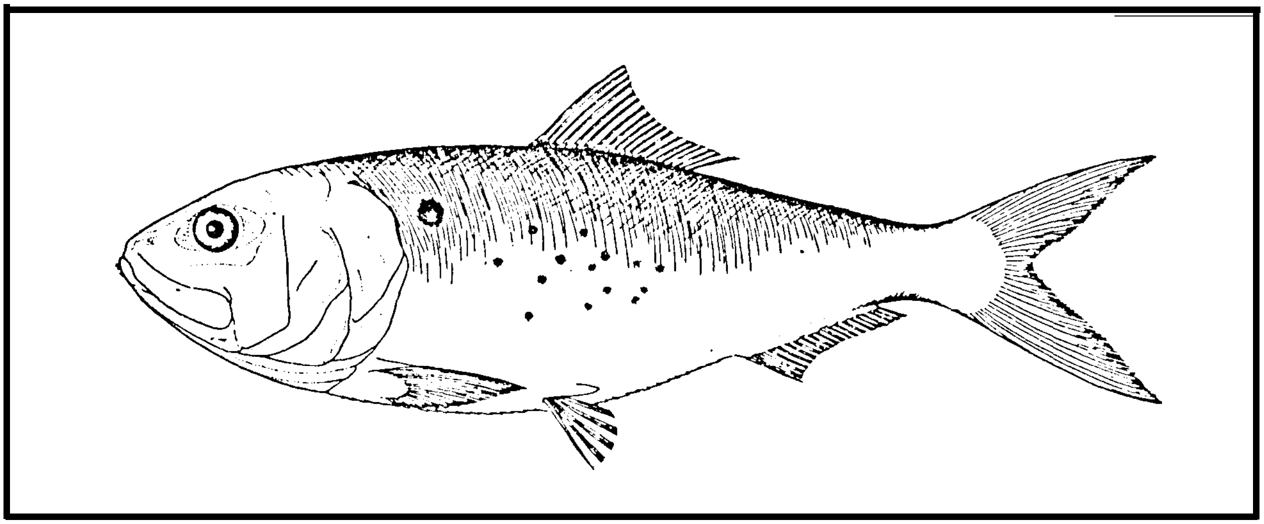

Figure 1. Atlantic menhaden.

ATLANTIC MENHADEN

NOMENCLATURE/TAXONOMY/RANGE

Scientific name .. <u>Brevoortia tyrannus</u>

Preferred common name .. Atlantic menhaden (Robins et al. 1980; Figure 1)
Other common names. . Pogy, mossbunker, bunker, fat-back, shad, bug-mouth
Class .... .Osteichthyes
Order .... .Clupeiformes
'Family ..... Clupeidae (herrings)

Geographic range: Temperate coastal waters from Nova Scotia to Jupiter Inlet, Florida; common in the Indian River City, Florida, gill net fishery (Dahlbert 1970). Atlantic menhaden are abundant all year in the South Atlantic Bight; spawning (December through February) occurs in shelf waters from Cape Lookout to New River Inlet, North Carolina. Concentrations of age 0 fish occur in inshore estuarine waters all along the Atlantic seaboard (Figure 2).

MORPHOLOGY/IDENTIFICATION AIDS

Branched dorsal rays, 16-17; branched anal rays, 16-23; pectoral rays, 15-17; pelvic rays, 7; gill filaments, 51-66; lateral line scales, 40-50; ventral scutes 28-35; vertebrae 45-50; body oblong and compressed with a thin belly wall; scales large, coarse, with long slender pectinations, strongly overlapping and in regular rows; predorsal scales on either side of median line enlarged; prominent radiating opercular striations; and pelvic fin rounded with innermost and outermost rays about equal length (Dahlberg 1970, 1975).

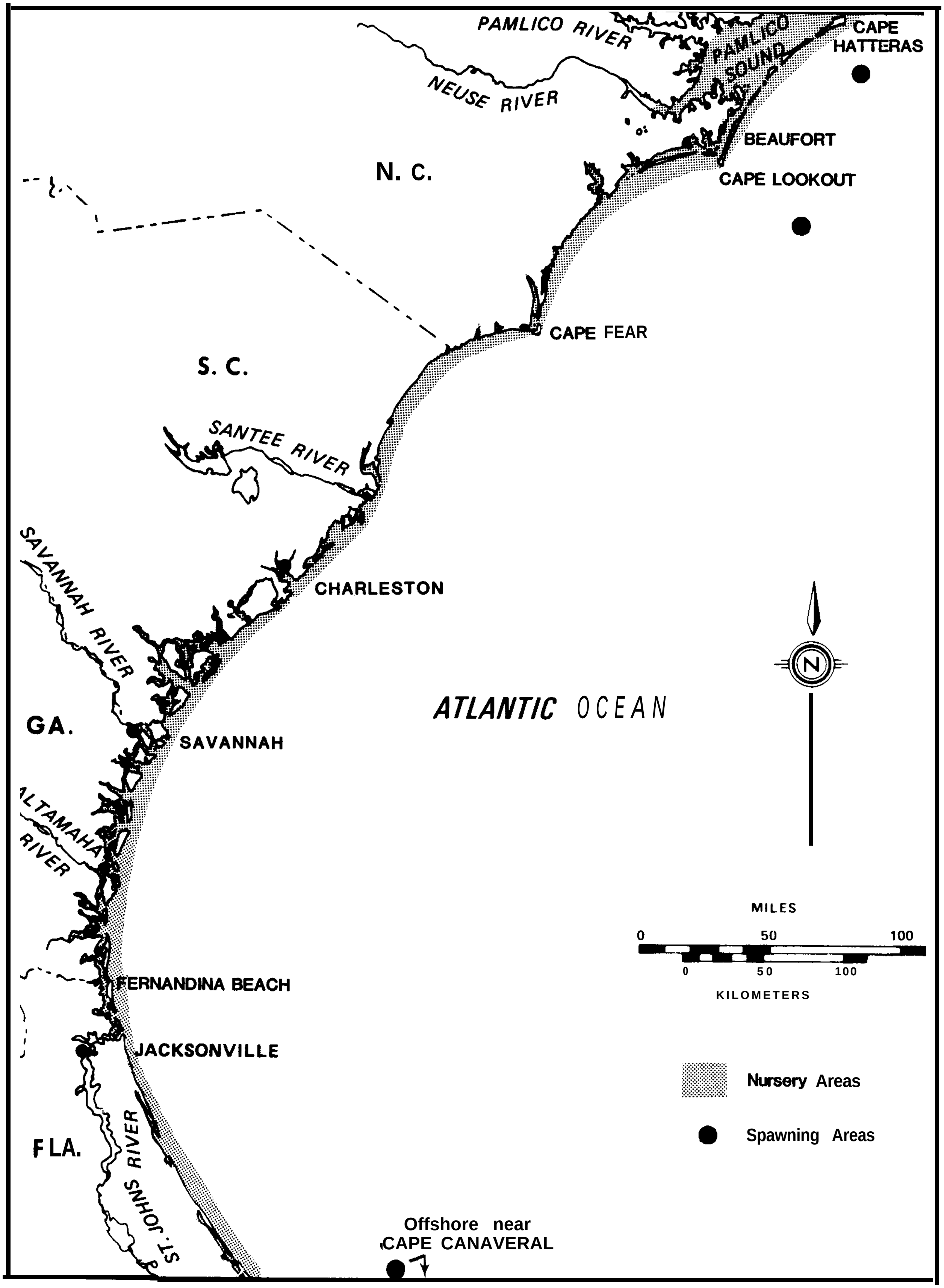

Figure 2. Distribution of the Atlantic menhaden in the South Atlantic Bight, Southeastern United States.

Color in life: green, brown, or blue-grey, darker on dorsal surface. A dark humeral spot may be followed posteriorly by a series of smaller spots which can fade readily upon capture. Brevoortia tyrannus can be distinguished from B. smithi (the only other Atlantic coast species) as having a frontal groove, larger coarser scales in regular rows (therefore, lower scale-related counts), pointed (versus rounded) scale pectinations, a row of lateral spots behind the humeral spot, more gill filaments on the ceratobranchial arch, rounded pelvic fins, opercular striations, and lacking a bright yellow caudal fin in life. Fresh B. tyrannus may have a darker anal fin and more body mucus than do B. smithi. Atlantic menhaden can be distinguished from F_1 hybrid Atlantic menhaden (Brevoortia smithi x B. tyrannus) as having a longer frontal groove, lateral spots (absent to few in hybrid), and a rounded ventral fin. Dahlberg (1970, 1975) provided additional measurements and descriptions of qualitative characters. Jones et al. (1978) gave detailed descriptions of Atlantic menhaden developmental stages (egg through adult).

REASON FOR INCLUSION IN SERIES

Atlantic menhaden constitute about 25% to 40% of the combined annual landings of Atlantic coast and Gulf of Mexico menhaden species, which collectively comprise the largest commercial fishery by weight in the United States. They are important prey items for many other fish species and are seasonally important components of estuarine and shelf fish assemblages. Atlantic menhaden depend on these habitats during their entire life cycle and utilize estuarine zones as nursery areas. Due to the species' great abundance and extensive migration patterns, the Atlantic menhaden likely influences the conversion and exchange of energy and organic matter within biological systems throughout its range.

LIFE HISTORY

Terminology used to describe life history stages conforms to that used by Lewis et al. (1972) and Moyle and Cech (1982).

Adult Migration and Spawning

Knowledge of timing and location of spawning has been obtained from collections of extremely ripe or spent adults (Higham and Nicholson 1964; June 1965; Dahlberg 1970) as well as eggs and larvae (Reintjes 1961, 1968; Herman 1963; Kendall and Reintjes 1975; Ferraro 1980b). Data on movement and population age or size structure have been obtained from distribution of purse-seining effort (Roithmayr 1963), length/weight/age frequencies in catches (June and Reintjes 1959; Nicholson 1971, 1972), and returns from extensive tagging experiments (Nicholson 1978). Atlantic menhaden undergo extensive north-south seasonal migrations and inshore-offshore movements along the Atlantic seaboard. Schools include fish of similar size and age. Migration patterns are also related to spawning habits, and some spawning occurs every month of the year in waters ranging from estuaries to the edge of the Continental Shelf.

Fish of all ages congregate just south of Cape Hatteras, North Carolina, from November through March and spawn there in shelf waters from 100 to 200 m (328 to 656 ft) deep, probably within 70 m (230 ft) of the surface (Reintjes and Pacheco 1966). The heaviest spawning is off Cape Lookout, North Carolina, from December through February. Adults then move inshore and northward in the spring and stratify by age and size along the Atlantic seaboard. Adult menhaden have been collected from estuaries and some move as far inshore as the brackish-freshwater boundary. The oldest and largest fish migrate the farthest, and some move as far north as the Gulf of Maine. Adults that remain in the South Atlantic Bight move southward to the northern part of Florida by" the fall. Representatives of all age classes return to the shelf waters of the South Atlantic Bight in late autumn.

During migration, spawning occurs progressively closer inshore, and in the late spring some fish spawn within the coastal embayments of the North Atlantic region. The lack of significant spawning to the north and east of Nantucket Shoals (Colton et al. 1979) could be due to the reduced numbers of fish in those areas during the years sampled or a lack of sampling effort in appropriate locations. There are definite spring and fall spawning peaks in the Middle and North Atlantic regions, and some spawning occurs during the winter in the shelf waters of the Middle Atlantic Bight. Temporal and spatial segregation of spawning activity provides a mechanism for the existence of races (= subpopulations; see The Fishery section). Higham and Nicholson (1964) speculated that a female may spawn more than once in a season. See the Environmental Requirements section for spawning temperatures.

The migratory habits of Atlantic menhaden south of Cape Canaveral, Florida, are unclear. Dahlberg (1970) reported that Atlantic menhaden in the vicinity of the Indian River, Florida, remain near- to inshore all year and spawn there during the winter, commonly hybridizing with the yellowfin menhaden (Brevoortia smithi). Reintjes (1961) collected large numbers of Brevobrtia eggs and larvae from shelf waters between Cape Canaveral. and Jupiter Inlet, Florida, in February, but was unable to identify them to species. No Atlantic menhaden from south Florida waters have ever been tagged (Nicholson 1978), but hybrid Atlantic menhaden and yellowfin menhaden have been collected as far north as Sapelo Island, Georgia, and Beaufort, North Carolina, respectively, during the summer (Dahlberg 1970).

Fecunditv

Higham and Nicholson (1964) reported values of 38,000 to 631,000 ova/fish while June (1961a) gave values of 40,000 to 700,000 ova/fish, with both sets of estimates depending on the size of the fish. Dietrich (1979) reported fecundities of 116,000 to 568,000 ova/fish for age I to age V females, respectively (Table 1). Higham and Nicholson (1964) gave the following equation for the estimation of fecundity (F: ova/fish)

$$\log F = 7.2227 + (0.0176)(\text{fork length, mm})$$

$$r^2 = 0.726$$

while Dietrich (1979) gave the following equations:

$$F = (488)(\text{wet body weight less ovaries, g})$$
$$r^2 = 0.916$$
$$F = (92592)(\text{age, years})$$
$$r^2 = 0.879$$
$$\log F = 8.6463 + (0.0120)(\text{fork length, mm})$$
$$r^2 = 0.871$$

See Dietrich (1979) for a comparison of the results. The reproductive potential of the Atlantic menhaden stocks dropped by at least an order of magnitude between 1955 and 1978 because of a severe reduction in the numbers of fish of reproductive age (Dietrich 1979; see The Fishery section); but relationships between recruitment and numbers of spawners have not been documented.

Eggs and Larvae

Eggs of the Atlantic menhaden are pelagic and have been reported to hatch at 2 days (Kuntz and Radcliffe 1917; no temperature specified), 2.9 days at 15.5" C (60" F) (Ferraro 1980a), and at 2.5 to 2.9 days at an

Table 1. Fecundity-at-age for Atlantic menhaden (Dietrich 1979).

Age	Number of eggs per female (thousands) Mean	Range	Sample size
I	115.8	26.5 - 250.7	21
II	177.4	39.2 - 368.8	34
III	302.8	127.7 - 458.3	33
IV	308.6	142.7 - 514.0	12
V	568.4	—	1

average temperature of 15.5" C (60" F) (Hettler 1981).

Survival of Atlantic menhaden embryos to hatching is very low (2.0% to 45.4%) with 48.7% to 94.0% of the deaths occurring before blastopore closure (Ferraro 1980a). See the Environmental Requirements section for the factors influencing embryonic survival.

Atlantic menhaden larvae begin feeding on individual zooplankters (Reintjes and Pacheco 1966) about 4 days ä 'ter hatching, when the yolk sac is close to total absorption, the eyes are pigmented, and the mouth is functional (Hettler 1981). Larvae enter estuaries after 1 to 3 months. at sea (Reintjes 1961) at lengths of 14 to 34 mm fork length (FL) (Reintjes and Pacheco 1966) with those longer than 30 mm FL already metamorphosing to the adult morphology (Lewis et al. 1972). This occurs from May through October in the North Atlantic region, October through June in the Middle Atlantic Bight, and December through May in the South Atlantic Bight (Reintjes and Pacheco 1966). As they grow, the larvae probably feed on progressively larger zooplankters (Kjelson et al. 1975).

Young fish move into the shallow portions of estuaries including river shoals and the heads of small tidal creeks (Massman 1954; Massman et al. 1954; June and Chamberlin 1959; Pacheco and Grant 1965; Wilkens and Lewis 1971; Lewis et al. 1972; Weinstein 1979; Weinstein et al. 1980). Here they continue to grow and metamorphose through a prejuveni 12 stage into juveniles (see Growth Characteristics section) Young-of-the-year and yearling menhadenmove out of estuarine creeks and channels onto the surface of the salt marsh during high tides (Targett, unpublished MS.'). Several studies have reported abundances of young menhaden that were higher in those portions of estuarines with the lowest salinity (<5 ppt) (Lewis et al. 1972; Weinstein 1979; Weinstein et al. 1980). Massman et al. (1954) reported abundances of prejuveniles that were higher above the brackish-freshwater boundary than below, and Rogers et al. (unpublished MS.[2]) have shown that this pattern persiscs during high river discharge.

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[1]Targett, T. E. High tide movement of juvenile Atlantic menhaden (Brevoortia tyrannus) onto the surface of Spartina salt marshes in Southeastern United States estuaries. Skidawav Institute of Oceanography, Savannah", Georgia.

[2]Rogers, S. G., S. B. Van Sant, and T. E. Targett. Utilization of Southeastern USA salt marsh estuaries by fishes as nursery ground: the influence of springtime freshwater. conditions. Ski daway Institute of Oceanography, Savannah, Georgia.

A "critical period" of survival in young fishes was first defined by Hjort (1914) and discussed for clupeiform fishes by Schumann (1965) and May (1974). Menhaden hatch out in an undeveloped state as do most fishes with high fecundity and little parental care. Such fish usually are inefficient feeders although there is frequently a rise in efficiency with growth (Schumann 1965). Feeding in the youngest *Clupea*, *Engraulis*, and *Sardinobs* larvae depends largely on food availability in that they will eat to capacity in the presence of high food concentrations and starve in the absence because of their inability to move about in search of food. A routine search pattern is initiated only upon encounter and/or capture of a food particle. Given the heterogeneity in distribution of pelagic plankters and the inability of many clupeiform fishes to cope with low food concentrations, menhaden likely have a critical period of larval survival. It is possible that year-class strength is partially determined during this period. The critical period probably occurs when larvae are spawned offshore or swept offshore after having been spawned nearshore. Individual larval condition factors (weight/length ratio) increase rapidly upon entering an estuary (Lewis and Mann 1971).

Data that link survival at yolk sac absorption to year-class strength do not exist for any fish, nor do quantitative estimates of mortality from predation on and starvation by fish larvae (May 1974). Minimum food concentration for inception of feeding activity is not known. and survival curves do not exist for larval Atlantic menhaden. Nelson et al. (1977), however, developed an environment-recruit model in an attempt to explain variation in year-class strength. Since larval menhaden are thought to depend largely on wind-driven (Ekman) transport to reach estuarine nursery grounds (particularly in the Middle and South Atlantic Bights), the model incorporated the known spawning times and locations, year/time/location-specific wind vectors, year/time-specific discharges of major tributary systems, and the minimum sea surface teniperdture at the mouth of Delaware Bay. A survival index was calculated as the ratio of observed recruitment to the fishery (age I) to that predicted by a Ricker (1954) spawner-recruit (density-dependent) model. The magnitude of the index "should reflect those environmental [density independent] effects which influence survival of menhaden from the time of spawning to the time of recruitment to the fishery age I" (Nelson et al. 1977). The model explained 84% of the variation in the survival index for the years investigated (1961-71) with Ekman transport being the principal component. The correlation has not been as strong in recent years (Robert B. Chapoton, National Marine Fisheries Service [NMFS], Beaufort, North Carolina; pers. comm. 1982) perhaps because of the increased importance of northern-spawning fish (see The Fishery section). Vaughan (1977) also suggested that unpredictable natural events, such as storms, regulated survival to age I.

Estimates of survival to recruitment (age I) do exist and are based on reproductive output at a given stock size and age structure from catch data compared to the relative contribution to the landings by age I fish the following year. Nelson et al. (1977) gave estimates that ranged from 26.8 to 159.1 fish/1×10^6 eggs spawned (1955-71), and Dietrich (1979) estimated 78 to 282 fish/1×10^6 eggs spawned.

Juveniles and Adults

Metamorphosis marks a change from a visual mode of feeding to a non-selective, filtering mode (June and Carlson 1971; Durbin and Durbin 1975). This shift is accompanied by a loss of teeth, an increase in the number and complexity of gill rakers, and an increase in the complexity and musculature of the digestive tract (June and Carlson 1971). Prejuveniles are somewhat intermediate in feeding mode (June and Carlson 1971) and body structure (June and Carlson 1971; Lewis et al. 1972). See the Growth Characteristics section for concurrent changes in growth characteristics.

Juveniles begin congregating into dense schools as they leave shoal areas. Most emigrate from estuaries from August through November (earliest in the North Atlantic region) at lengths reported by June (1961a) of 55 to 150 mm FL and by Nicholson (1978) of 55 to 140 mm total length (TL), who stated that most emigrants are between 75 and 110 mm TL. Based on the results of extensive tagging, many age 0 fish migrate to the North Carolina fall fishery between Cape Lookout and New River Inlet (Nicholson 1978). Fish in the southernmost portion of the South Atlantic Biqht, however, exhibited less offshore migration (Dahlberg 1970), and tagging results indicated that juveniles leaving the estuaries of the South Atlantic Bight and the North Atlantic region may not move very far north or south during their first year (Nicholson 1978). Larvae entering estuaries late in the season may remain within the estuary one additional year and emigrate at age I. Some juveniles and adults are found in sounds and bays along the South Atlantic Bight during mild winters (June 1961a). Fish exiting estuaries everywhere along the Atlantic seaboard eventually disperse throughout most of the geographic range (Nicholson 1978).

Most Atlantic menhaden reach maturity by age II. About 10% of the age I fish and 90% of the age II fish were found to be capable of spawning (Higham and Nicholson 1964). Fish from age 0 up, however, are found in the migrating schools. Fish older than age IV are rare in the commercial catch even though they can live 8 to 10 years (June and Roithmayr 1960). Atlantic menhaden are well adapted for an active, migratory existence with their large lipid reserves,' torpedo-like body shape, and copious body mucus (Dahlberg 1970). Menhaden suffocate rapidly when captured.

GROWTH CHARACTERISTICS

Growth rates vary among years and throughout the species' range (June and Reintjes 1959, 1960; June 1961b; June and Nicholson 1964; Nicholson and Higham 1964a, 1964b, 1965; and Nicholson 1975). The age of Atlantic menhaden can be determined from scale markings (=annuli) (McHugh et al. 1959; June and Roithmayr 1960; Kroger et al. 1974).

Fish of the same age are progressively larger in more northerly fisheries (Nicholson 1978), but mature at smaller sizes in more southerly areas. Fish in the South Atlantic Bight matured at a minimum length of 180 mm FL ($\bar{x}$ = 230) while those in the Middle Atlantic Bight matured at a minimum of 210 mm FL ($\bar{x}$ = 225) (Higham and Nicholson 1964). Evidence indicates that growth rates have changed in response to fishing pressure, with fish of the same age being larger in the late 1960's and early 1970's than in the late 1950's and early 1960's (Nicholson 1975).

Growth has been shown to be allometric in larval, prejuvenile (Lewis et al. 1972), juvenile (Lewis et al. 1972; Epperly 1981), and adult stages. Three different "stanzas" of growth in young menhaden were reported by Lewis et al. (1972), with inflection points at 30 and 38 mm TL (70 and 469 mg wet weight). These points served as the basis for their division of the life history stages. Lewis et al. (1972) cited an unpublished manuscript that stated that the relationship between length and weight is similar for juveniles and adults. Conversion from length to weight can be made using the appropriate equation in Table 2.

Table 2. Weight-length regressions for Atlantic menhaden (Lewis et al. 1972; Epperly 1981*). log, weight = a + b (log, length).

Location	Measurement units		a	b
	Weight	Length		
White Oak River Estuary, North Carolina				
Larvae (up to 30 mm TL)	mg wet	mm TL	-8.110	3.605
Prejuveniles (30 to 38 mm TL)	mg wet	mm TL	-16.964	6.308
Juveniles (38 mm TL up)	mg wet	mm TL	-5.230	3.145
Fall and winter spawners & offspring (Middle, S. Atlantic Bights)*	g wet	mm SL	-10.884	3.067
North Atlantic spring spawners and offspring*	g wet	mm SL	-11.240	3.145
Middle Atlantic spawners and offspring*	g wet	mm SL	-11.037	3.103
South Atlantic spawners and offspring*	g wet	mm SL	-10.579	2.995

Atlantic menhaden growth begins in the spring and ends in the fall as the water temperature crosses an approximate 15" C (59" F) threshold (Beaufort Inlet, North Carolina) (Kroger et al. 1974). Age 0 fish ranged from 40 to 185 mm TL at the end of the growing season. depending on when they were spawned and entered the estuary. The smallest fish had not yet formed their first growth annulus. Young of the next year class arrived in the spring only 20 to 30 mm TL shorter than the smallest fish of the previous year class. These factors, combined with a faster larval growth rate (Lewis et al. 1972; Kroger et al. 1974) and latitudinal differences in growing season, probably explain the observed differences in sizes of fish of the same "age" within a single year's catch.

Atlantic menhaden reach lengths of about 500 mm TL and weights of 1500+ g at ages of 8 to 10 years. Cooper (1965) collected an 8-year-old fish that measured 470 mm TL and 1,674 g wet weight.

THE FISHERY

History

The Atlantic menhaden fishery was first established in the late 1600's or early 1700's to obtain fish for agricultural fertilizer (Frye 1978). In the early 1800's, an industry was first developed to obtain oil from menhaden (Goode 1879; Goode and Clark 1887), and with increased use of oil products, there were 90 reduction plants in North Carolina alone by 1869 (June 1961a). Today this species contributes 25% to 40% of the landings in the largest commercial fishery (by weight, Brevoortia species) in the United States. Annual landings for 1979 through 1981 averaged about 400,000 metric tons and $38 million dollars in market value (NMFS 1980, 1981, 1982). Plants that process Atlantic menhaden products currently operate from Maine to Florida. Ninety-six percent to 98% of the catch is sold to fertilizer, livestock, and cosmetic interests as fishmeal, soluble proteins, and oils; the remainder is used in pet food products and as fish bait (NMFS 1980, 1981, 1982). The majority of the landings is by purse seine. Federal efforts to develop data for management of Atlantic menhaden began in 1955 (June 1957).

The Catch

The Atlantic menhaden fishery has two annual phases: a summer and fall fishery from Maine to central Florida and an intensive fall and winter fishery off North Carolina between Cape Lookout and New River Inlet (June 1961a; Nicholson 1978). The fishery exploits fish of ages I -VII, but fish of ages I-III account for 85% to 90% of the total catch (June 1961a; Nicholson 1975). During the summer and fall, fish caught in the South Atlantic Bight are mostly ages I and II (>99% of the landings) with the north Florida fishery composed mostly of age I fish. Concurrently, fish in the Chesapeake Bay area and the southern portion of the Middle Atlantic Bight are also age I and II although they are longer 'and heavier on the average. Some age III and IV fish are present in an early spring pound net fishery in Chesapeake Bay. Most of the fish caught in the northern portion of the Middle Atlantic Bight are age II and III, the age II fish being larger than those to the south. The North Atlantic fishery operates from mid-June through October and primarily exploits age III or older fish. The purse seine fishery north of Cape Hatteras is over by late November. Age 0 fish begin to be vulnerable to the fishery during late fall and winter from Chesapeake Bay south. The North Carolina fall fishery is composed of all age classes.

Atlantic menhaden stocks were drastically reduced during the 1960's. Landings dropped from 671,400 metric tons in 1955 to around 200,000 metric tons per year from 1966 through 1969 (Nelson et al. 1977). As the population size decreased, the age structure also changed. Fish older than age III became scarce and fish older than age IV were practically nonexistent even in the North Carolina fall-winter fishery. Northern plants, especially those in the New England area which had depended on age III and IV fish, closed down (Nicholson 1975). Age I and II fish constituted the bulk of the landings and age 0 fish became more important both absolutely and relatively (Nicholson 1975). The stocks began to recover in the early 1970's, with age III fish again appearing in North Atlantic catches. The first significant Maine landings (3100 metric tons) since the 1960's occurred in 1973 (NMFS 1973, 1974, 1975; Nelson et al. 1977). Catches continued to improve into the early 1980's; however, the size of the reproductive stocks (ages III through IV) remain low (Atlantic Menhaden Management Board [AMMB] 1981).

Management

More than 50% of the annual landings of Atlantic menhaden are from within State territorial waters, mostly from the Chesapeake Bay area (Robert B. Chapoton, NMFS, Beaufort, North Carolina; pers. comm. 1982). This fact, combined with the migratory nature of the species and the dependence of northern fisheries on escapement of age I and II fish from fisheries in the South Atlantic Bight and Chesapeake Bay (Nicholson 1978), makes regulation a compromise situation between the industry and Federal and State agencies.

The stocks have generally been unmanaged except for establishment of local vessel quotas to protect the market. Nelson et al. (1977) suggested that the fishery is somewhat self-regulating in that reduced catches bring about reduced effort and plant closures, allowing the stocks to recover. They stressed that proper management practices could reduce the chance of repeating the mistakes of the past and prevent a crash in the fishery. In addition, Schaaf (1975) pointed out that "allowing the fishery to be controlled . ..by the economics of free market competition...assures that (1) the average profit for the whole industry will be zero... and (2) there is no mechanism to provide for protection of the resource, since if either costs go down or value goes up new effort can afford to enter the fishery and eventually may exceed the BBEP [Biological Break-Even Point, a point at which the fishery collapses]." Schaaff (1975) also warned that the level of effort that caused the fishery to collapse in the 1960's could be maintained even if catches dropped to 200,000 metric tons/year because of higher product prices during the mid-1970's. He urged the implementation of a flexible quota system coordinated by the Atlantic States Marine Fisheries Commission (ASMFC) that would allow the stocks to continue to rebuild while effects of effort requlations are studied. The various States have now endorsed an ASMFC management plan (AMMB 1981) that is awaiting enactment by various State legislatures (Robert B. Chapoton, NMFS, Beaufort, North Carolina; pers. comm. 1982). See the AMMB (1981) document for specific management goals as well as additional social and biological information. In spite of the difficulties involved in managing such a complex shared resource, the prospects of developing a workable management plan are good (Schaaf 1975).

Maximum sustained yield (MSY) from historic catch-effort data has recently been estimated by Schaaf and Huntsman (1972) at 600,000 metric tons/year and by Schaaf (1975) at 560,000 metric tons/year. Estimates incorporating the use of a Ricker (1954) spawner-recruit (density-dependent survivorship) model were given as 380,000 metric tons/year by Schaaf and Huntsman (1972) and averaged 419,000 metric tons/year based on known survivorship (1961-71) (Nelson et al. 1977). The recruit-environment model developed by Nelson et al. (1977) (see the Life History section) likewise averaged 419,000 metric tons/year (1961-71) and is proposed to offer a way of "fine-tuning" predicted catch on a yearly basis by constantly updating yield estimates. The vulnerability of the Atlantic menhaden fishery to fluctuations in year class strength was first pointed out by June (1961a). It has since been stressed that the maintenance of a healthy stock of spawning-age fish (III to VI) should be a primary concern of management efforts (Schaaf and Huntsman 1972; Schaaf 1975; Nelson et al. 1977; Vaughan 1977). Good stocks of spawning age fish would bring multiple benefits including higher reproductive potential (decreasing the impact of years with poor recruitment conditions), decreased vulnerability to weak year classes, and increased weight of landings due to a higher contribution of older fish to the catch.

Annual instantaneous natural mortality was estimated at 0.36 (1955-64) by Schaaf and Huntsman (1972) and at 0.42 for the 1955 year class by Nelson et al. (1977). Their respective estimates of annual instantaneous fishing mortality were 0.82 to 2.14 (1955-64) and 0.36 for the 1955 year class. A combination of these data yields total instantaneous mortality estimates ranging from 1.18 to 2.56, which correspond to total annual mortality rates of 69.3% to 92.3% (ages I through VI).

Subpopulations

Because a genetically distinct stock can have its own homogeneous vital parameters of recruitment, growth, and mortality (Cushing 1968), identification of the stock (=subpopulations) and stock-specific biological traits is necessary for proper management. Various authors have proposed the existence of two to five Atlantic menhaden subpopulations based on meristic and morphometric comparisons (June 1958, 1965; Sutherland 1963; Higham and Nicholson 1964; June and Nicholson 1964; Dahlberg 1970). Dahlberg (1970) reported a distinct subpopulation of Atlantic menhaden south of Cape Canaveral in the vicinity of the Indian River, Florida. Nicholson (1978) stated that the extensive north-south migrations, latitudinal stratification by age and size in the summer, and intermingling of all age classes south of Cape Hatteras in the winter preclude the existence of more than one stock. Epperly (1981), however, provided electrophoretic as well as meristic and morphometric data that indicated significant differences between those fish spawned in the inshore waters of the North Atlantic during the spring and those spawned in the fall and winter in the South and Middle Atlantic Eights. The fall-spawning fish of the North Atlantic Bight and the spring-spawning fish of the Middle Atlantic Bight may also be distinct subpopulations, but this aspect has not been fully investigated.

ECOLOGICAL ROLE

Atlantic menhaden occupy two distinct types of feeding niches during their lifetime. As larvae they are size-selective plankton feeders and as juveniles and adults they are indiscriminate filter feeders. Data on the food of larvae before they enter the estuary do not exist, but Schumann (1965) reported that pteropod and bivalve larval stages plus crustacean nauplii comprised the diets of other larval clupeiform fishes. After entering the estuary, Atlantic menhaden larvae appear to be extremely selective for certain sizes and species of prey. Larvae from the Newport River Estuary, North Carolina, ranging from 26 to 31 mm TL ($\bar{x}$ = 29 mm TL), consumed copepods and copepodites of only four taxa, comprising 99% by numbers and volume of their gut contents (Kjelson et al. 1975). These prey items ranged from 300 to 1200 μm in length ($\bar{x}$ = 750 μm and were consumed despite an abundance of copepod nauplii, barnacle larvae, and small adult copepods in plankton tows. Larvae in the laboratory ignored all other food items including Artemia and Balanus nauplii when offered copepods (June and Carlson 1971). Larval menhaden in the Newport River Estuary fed primarily during daylight hours with one major burst of feeding activity, usually before noon (Kjelson et al. 1975).

Juvenile and adult Atlantic menhaden strain particulates from the water column with a complex set of gill rakers. The rakers can sieve particles from 13.2 to 1200 μm in size, which includes zooplankton, larger phytoplankton, and chain-forming diatoms. Biochemical analyses indicated that juvenile gut contents vary with pretype availability, decreasing in reliance on zooplankton from open waters to marsh habitats (Jeffries 1975). Atlantic menhaden may also be capable of utilizing epibenthic resources (Edgar and Hoff 1976). Peters and Schaaf (1981) speculated that the annual phytoplankton and phytoplankton-based production in east coast estuaries is not sufficient to support the juvenile Atlantic menhaden population during its residency. They proposed that the abundant organic detritus resource may be utilized.

The roles of Atlantic menhaden in systems function and community dynamics have received little attention. Larvae and juveniles are seasonally important components of estuarine fish assemblages (Tagatz and Dudley 1961; Cain and Dean 1976; Bozeman and Dean 1980). Estimates of the mean daily ratio for larvae range from 4.9% (Kjelson et al. 1975) to 20% (Peters and Schaaf 1981) of wet body weight. Assimilation of ingested energy exceeded 80% for plant and animal material (Durbin and Durbin 1981). Given the tremendous numbers, individual growth rates, and seasonal movements of these fish, they are consuming and redistributing a large amount of energy and materials on an annual basis, including exchanges between estuarine and shelf waters.

Kjelson et al. (1975) noted that the copepod taxa preferred by larval menhaden and other species decreased from a mean value (2 years) of 81% to 48% of the total zooplankton biomass during the period of larval residence. They speculated that this may be partially explained by larval feeding. Durbin and Durbin (1975) suggested that Atlantic menhaden in coastal waters may also alter the composition of plankton assemblages through grazing certain size ranges.

Bluefish (Pomatomus saltatrix), striped bass (Morone saxatilis), bluefin tuna (Thunnus thynnus), and sharks are important Atlantic menhaden predators (Reintjes and Pacheco 1966). Nothing is known of the impact of fish predation on menhaden populations.

ENVIRONMENTAL REQUIREMENTS

Temperature, Salinity, and Dissolved Oxygen

Field data indicate that Atlantic menhaden occur throughout a wide range of physicochemical conditions. Several studies have raised questions regarding the limits of tolerance and optimum conditions. June and Chamberlin (1959) and Reintjes and Pacheco (1966) reported that larval menhaden did not enter estuarine waters at temperatures below 3" C (37" F). Many studies have noted an affinity of young menhaden for low salinity waters (see the Life History section). Wilkens and Lewis (1971) speculated that larval menhaden require low salinity water to metamorphose properly, and Lewis (1966) found that although larvae metamorphosed in salinities of 15 to 40 ppt, one-third of the juveniles developed slightly crooked vertebral columns. Larvae held in the laboratory at 25 to 40 ppt, however, metamorphosed completely with no abnormalities (Reintjes and Pacheco 1966), and larvae trapped in a natural cove at Beaufort, North Carolina, transformed into juveniles at 24 to 36 ppt (Kroger et al. 1974). Salinity does affect temperature tolerance, activity, metabolism, and growth. Lower salinities decreased survival at temperatures below 5" C (41" F), and survival was poor at 6° C (43" F) in freshwater (Lewis 1966). The effect of salinity on upper temperature tolerance was not significant (Lewis and Hettler 1968). Larvae that Hettler (1976) reared at 5 to 10 ppt exhibited significantly higher activity levels, metabolic rates, and growth rates than those reared at '28 to 34 ppt. Lewis (1966) also noted slower growth at high salinities.

Salinities of 10 to 30 ppt had no effect on developing embryos although temperature did (Ferraro 1980a). Embryonic mortality was significantly higher at 10" C (50" F) than at 15°, 20°, and 25" C (59°, 68°, and 77" F). Temperatures less than 7" C (45" F) were fatal to developing embryos. Time to hatching was significantly shorter at each progressively higher temperature. Surface temperatures in the spawning areas of the South Atlantic Bight during the months of highest egg capture are generally 12" to 20" C or 54" to 68" F (Walford and Wicklund 1968). The lowest temperatures at which Atlantic menhaden eggs and larvae have been collected in the North Atlantic region are between 10" and 13" C or 50" and 55" F (Ferraro 1980a). The temperature range for the Middle Atlantic Bight was 0" to 25" C (32" to 77°F), but most eggs and larvae were collected at 16" to 19" C or 61" to 66" F (Kendall and Reintjes 1975).

The limits of larval temperature tolerance are also affected by acclimation time. Survival above 38 C or 86' F (Lewis and Hettler 1968) and below 5" C or 41" F (Lewis 1965) was progressively extended by acclimation temperatures closer to test values. This implies that rapid changes to extreme temperatures are more likely to induce lethal effects than prolonged exposure to slowly changing values.

Hettler and Colby (1979) demonstrated that photoperiod at least partially explains variation in resistance to heat stress. Median lethal time increased linearly with photoperiod at 34" C (93" F). They also speculated that it may be important to other types of physiological stress. Lewis and Hettler (1968) observed increased survival of juveniles at 35.5" C (96" F) with increased dissolved oxygen (DO) saturation. Burton et al. (1980) found a mean lethal DO concentration of 0.4 mg/l, but they warned against interpretation of this value as 'safe" in view of the interactive nature of environmental factors. Westman and Nigrelli (1955) observed mass mortalities from gas embolism only in areas with highly variable salinity and organic pollution to a degree which made shellfish unfit for human consumption. Lewis and Hettler (1968) observed decreased survival at high temperatures by fish whose gill condition was affected by parasitism. The interactive nature of environmental factors must be considered when defining the healthy ranges of an organism.

Substrate and System Features

The association of the Atlantic menhaden with estuarine and nearshore systems during all phases of its life cycle is well documented. It is evident that young menhaden require these food-rich waters to survive and grow (see above discussion) and the fishery is concentrated near major estuarine systems (June 1961a). The relative importance, however, of different habitat types (i.e., sound, channels, marshes) and salinity regimes has received little detailed attention (see Life History section).

Environmental Contaminants

In a study of chlorinated hydrocarbon residues in Atlantic and Gulf of Mexico menhaden fishery products, Stout et al. (1981) showed that overall levels have decreased since the late 1960's, although significant differences between years for levels of polychlorinated byphenyls (PCB's) in the South Atlantic Bight and for dieldrin in the Middle Atlantic Bight could not be demonstrated. There was also a general lack of significant differences between areas within years, possibly due to the sampling regimen. They speculated that PCB levels have remained somewhat high because of leakage from sources established prior to regulation and continued allowance of limited specialty uses. Menhaden oil products carry the highest concentrations of such nonpolar compounds, and some samples contained levels in excess of United States Food and Drug Administration temporary tolerances as of 1977. Warlen et al. (1977) demonstrated that ^{14}C-DDT uptake by Atlantic menhaden is dose-dependent, with an assimilation value between 17% and 27%. Application of their model to field data suggested that uptake was via plankton and/or detritus. Little information exists about the toxicity of contaminants to Atlantic menhaden.

Other Factors

The seasonal depth distribution of Atlantic menhaden is tied to migration patterns. There are some fish in depths from 1 to 200 m (3 to 656 ft) on a year-round basis. The major distributions are presented in the Life History section. See that discussion for information on how water movement affects survival and transport of the young. The role of turbidity in Atlantic menhaden biology apparently has not been studied. Rogers et al. (unpublished MS.[2]) proposed turbidity along with salinity and nutrient gradients as means for young fishes locating estuarine areas along the Georgia coast. A similar proposition was made by Blaber and Blaber (1980) for young Australian fishes.

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16. Abstract (Limit: 200 words)

Species profiles are literature summaries of the taxonomy, range, life history, environmental requirements, and significance of coastal aquatic species. They are prepared to assist in environmental impact assessment. The Atlantic menhaden, Brevoortia tyrannus, contributes 25% to 40% of the landings of the largest commercial fishery (by weight) in the United States. Landings for 1979-81 averaged about 400,000 mt (440,920 t) and $38 million annually. All ages are important prey for many fishes and birds; the species is a seasonally important and migratory component of estuarine and shelf fish assemblages. In the South Atlantic, major spawning occurs from December through February near Cape Hatteras, North Carolina, in shelf waters that are 100-200 m (328-655 ft) deep. Larval Atlantic menhaden feed on zooplankton and move shoreward to estuaries after 1-3 months at sea. With growth, the juveniles gradually change to a less-selective, filter-feeding mode and generally migrate from estuaries to open shelf areas during late fall. Fish that exit estuaries everywhere along the Atlantic seaboard eventually disperse throughout the species' range. Atlantic menhaden occur in a broad range of temperatures and salinities. Larvae move toward low-salinity areas upon entering estuaries, and prejuveniles are dependent on low-salinity marsh habitats and river shoals for nurseries.

17. Document Analysis a. Descriptors

Estuaries
Fishes
Growth
Spawning
Feeding

b. Identifiers/Open-Ended Terms

Atlantic menhaden
Brevoortia tyrannus
Salinity requirements
Habitat requirements
Life history
Environmental requirements

c. COSATI Field/Group

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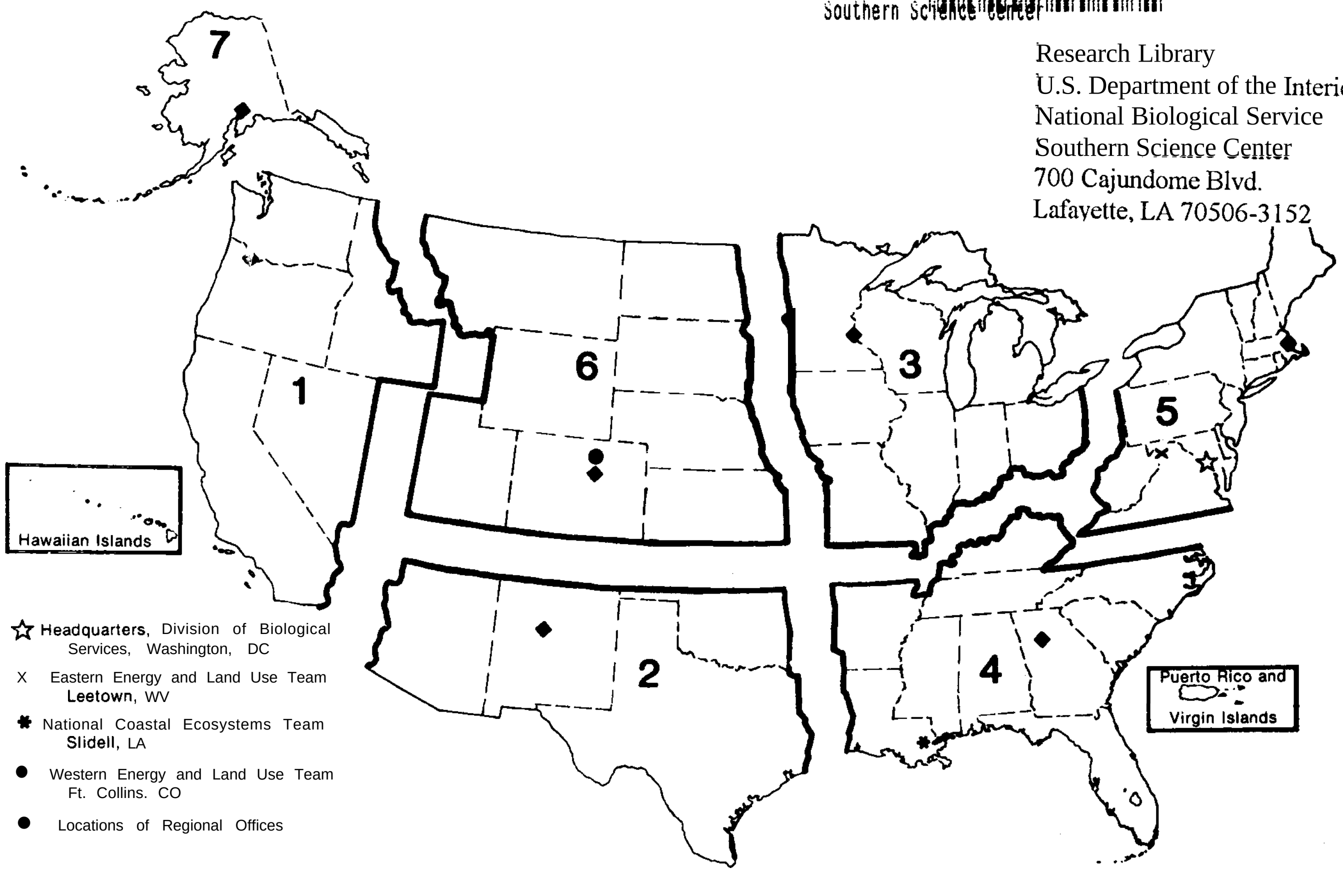

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